PREMOTOR CIRCUIT TOPOLOGY AND
SENSORY-MOTOR PATTERN SELECTION

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Abstract - **In recent years, modeling of ocular premotor circuits in the brainstem has unmasked several advantages linked to the topology of these circuits. In particular, their bilateral symmetry can implicitly provide for rich motor behavior in response to sensory patterns such as 1) coordination of vergence and version trajectories in binocular systems, 2) simple fusion of multiple sensory sources with diverse dynamics, 3) automatic selection of appropriate motor responses and platform coordination, according to bilateral sensory patterns (e.g. ocular vergence during linear fore-aft motion vs conjugate responses during inter-aural translation), and 4) use of parameter (circuit) switching to enable additional modes (e.g. saccades vs slow tracking). Spinal premotor pathways also include many levels of symmetry in the circuits controlling limb muscles, for example in the stretch reflex connections of agonist/antagonist muscle groups. These therefore imply a capacity to imbed *locally* several motor strategies, simply released by the current context and sensory inflow patterns. Hence circuit topology should be considered a key element in the process of sensorimotor mapping and in the selection of motor strategies. This is in contrast to the classical approach where desired motor patterns are selected at a cortical level, following several computational stages.**

Keywords – **Modelling, sensorimotor transformation, motor patterns, brainstem, spinal circuits, motor coordination.**

I. INTRODUCTION

In recent years, modeling of ocular premotor circuits in the brainstem has unmasked several advantages linked to the topology of biological control circuits. This paper will summarize the results obtained from the analysis of oculomotor reflex systems, and demonstrate a clear link with motor control in general.

In considering the mapping of sensory information to motor trajectories, the classical approach is to divide-and-conquer by separating the problem into sequential stages, e.g.:

1) Gathering 3-D sensory information from several modalities (visual, motion, motor, somatosensory), usually spatially distributed on neural maps,

2) Fusing the information into a common goal after correcting for differences in sensory dynamic processes (see Anastasio, this session),

3) Mapping the sensory coordinates of the 'goal' into motor (actuator) coordinates

4) Partitioning the task among available platforms,

5) Selecting the appropriate control strategy for each platform to achieve the goal, using forward and/or inverse models,

6) Sending the motor signals, as selected from stored control trajectories or from simpler dynamic compensators.

These are artificial boundaries, created by the computational demands. Furthermore, the sensory-motor mapping stages also include a need to move from spatial coordinates of the sensory signals into the temporally coded motor commands required by each plant. Some of this mapping is facilitated by placing sensory maps inside premotor feedback loops [9]. But it is not clear at what stage this is done in the computational sequence. Another issue is whether such computations must be duplicated in parallel for all possible movement strategies. It will be argued through examples from oculomotor control, that multiple motor strategies and sensory-motor mappings can be imbedded inside apparently simple and shared motor networks, provided they express in their topology the desired response 'modes'.
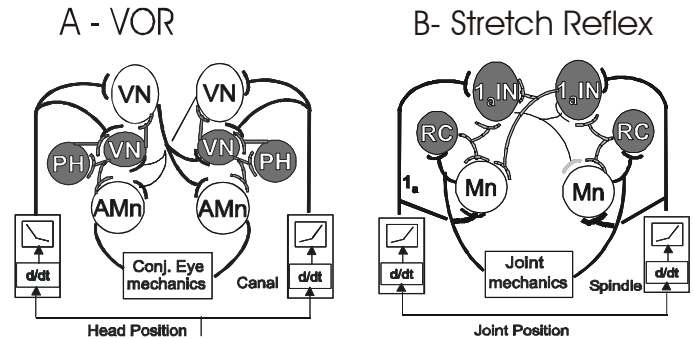

Fig. 1. Examples of symmetry in premotor pathways. A – Cells in vestibular nuclei (VN), prepositus hypglossi (PH) and abducens motor nuclei (AMn) in the brainstem. B- 1ₐ Interneurons (1_aIN), Renshaw cells (RC) and motorneurons (MN) of agonist-antagonist pair in spinal cord. Shaded cells are inhibitory; in both cases sensors (canal, spindle) are non-linear detectors of platform/joint velocity and project symmetrically with reciprocal (reversed) sensitivity.

II. MODES IN MOTOR NETWORKS

A Modes in a symmetric circuit

It is interesting that many premotor circuits have a high degree of topological symmetry. An example is provided for the major components of the vestibulo-ocular reflex (VOR, Fig. 1A) during compensation for head movement, and the stretch reflex in spinal agonist-antagonist networks (Fig. 1B). Some of the key factors are:

- Mirror-image symmetry in the topology across brainstem midline or between agonist-antagonist circuits
- Bilateral symmetry in matched sensory afferent projections (e.g. semicircular canals, spindles)
- Bilateral symmetry in motor projections (see section B below)

Anatomy and physiology support this type of interconnected symmetric structure [7, 8]. Models of the VOR using known neural topology have several advantages, extending beyond the classically assumed role of redundancy. Redundancy would follow from purely parallel processes; however these

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Abstract

Subject Terms

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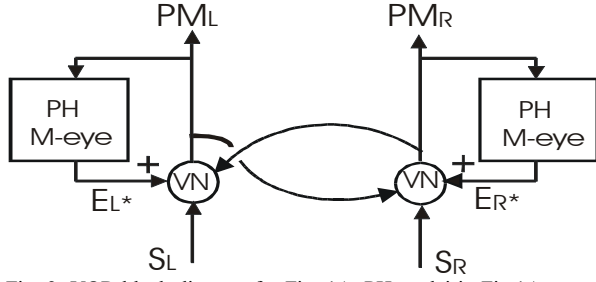symmetric circuits add interconnections between sub-processes which also increase response complexity.

Fig. 2: VOR block diagram for Fig. 1A. PH nuclei in Fig.1A are presumed to contain models of the eye plant (M-eye) so that each output can be an estimate of monocular eye position $E^*_{R,L}$ [1].

To illustrate, a simplified neural 'system' diagram for the VOR is presented in Fig. 2: the symmetry is restricted to mirrored topology across the midline and hence two modes are imbedded. These can be referred to as the common mode and difference mode (as in differential amplifiers) since they respectively process the sum and difference of sensory inflow.

If the M-eye processes on each side of Fig. 2 are simple first-order filters (time constant T), then

$$PM_R = \frac{(Ts+1)}{(T_cs+1)} G_c(S_R + S_L) + \frac{(Ts+1)}{(T_ds+1)} G_d(S_R - S_L)$$

$$PM_L = \frac{(Ts+1)}{(T_cs+1)} G_c(S_R + S_L) - \frac{(Ts+1)}{(T_ds+1)} G_d(S_R - S_L)$$

(1)

Two dynamic modes are now evident each with its own time constant (T_c and T_d) and associated gain factor. Any central premotor signal in this circuit will contain a linear combination of these two available modes. Clearly, judicious combination of left-right central signals can then be used to unmask the desired mode at motor (behavioral) levels.
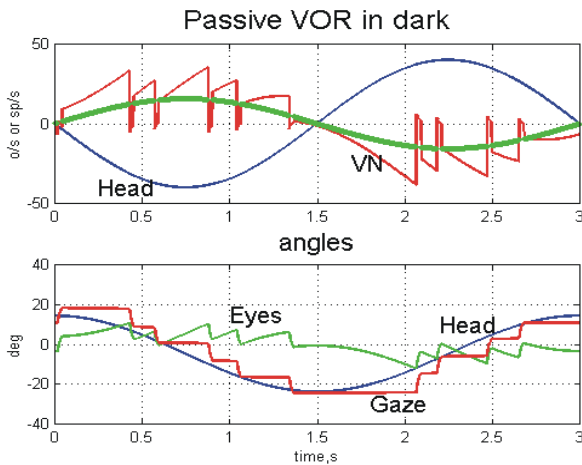

Fig. 3: Simulation of model in Fig.2, using pure conjugate drive (PM_L-PM_R) for both both eyes, and a different parameter set for each phase (see Galiana, IEEE TBME 38:532-543,1991)

The VOR contains two components observed in the eye response as nystagmus: slow phases opposite to head movement requiring a large central time constant (T_d), and fast (saccadic) phases reorienting the eyes in the orbit in the same direction as head velocity (with small time constant). Since the occurrence of saccades and fast phases is associated with on-or off-switching of special cells in the brainstem [10], the circuit in Fig.2 can generate nystagmus (alternating central dynamics) by simply assuming changes in the circuit weights for the two conditions. This approach has been successful in representing the nystagmus pattern of the VOR, as well as the qualitative pattern of firing rates on premotor cells in the VN (Fig. 3).

B Mapping Modes to Motor Patterns – Platform Coordination

In the angular VOR (head rotations), the premotor cells in the brainstem are excitatory from the vestibular nuclei (VN) to the contralateral abducens nucleus and inhibitory from the VN to ipsilateral abducens [e.g. 7]. Hence head rotation to the left excites the nerve from the left semicircular canal, inhibits that from the right canal, to cause excitation of the right abducens nucleus (AbN). Via interneurons in the AbN, there follows a contraction of both the lateral rectus of the right eye and medial rectus of the left eye. The result is both eyes turn to the right, opposite to the head turn (a conjugate eye movement or version). In terms of anatomy reflected about the (nasal) midline, we see an opposite response in both eyes, one towards the nose, the other towards the temple. It is therefore appropriate to choose an ocular coordinate system about the midline for horizontal eye movements: positive temporally and negative nasally. In this case, vergence is the negative sum of binocular angles, and version is the average difference:

Vergence = - (E_R + E_L)　　　　　　　　(2)

Version = (E_R – E_L)/2

The first question here is the coordination of the two eyes in the horizontal plane. Classically, it has been assumed that the circuits at the level of both VN control mainly conjugate eye movements, while separate circuits projecting directly to the oculomotor nuclei (medial rectus subdivision) control vergence. Thus, previous models of vergence control often rely on two parallel processors [e.g. 13]. Judging from Equ. 1 above, one would indeed expect pure conjugate ocular responses, if each eye received a pure difference between PM_R and PM_L in the bilateral circuit (as done in Fig.3). In fact, the projections from VN to motor nuclei from each side come from different cell populations, and have different weights. Furthermore, the neural activities observed at VN levels are affected by both vergence and version set-points. This implies shared control of these two modes (see reviews in [2]) .

In the bilateral structure, a simple example would rely on say weight 'a' from the contralateral PM and weight 'b' from ipsilateral PM, i.e.

E_R = [a PM_L - b PM_R] P(s)　　　　　　(3)

E_L = [a PM_R – b PM_L] P(s)

where   a > b >0, P(s) is the eye plant, and signs in Equ. 3 indicate excitation or inhibition. Substituing Equ. 1 into 3:

E_R = D_c(s) (S_R+S_L) – D_d(s) (S_R-S_L)　　　　(4)

$$E_L = D_c(s) (S_R+S_L) + D_d(s) (S_R-S_L)$$

where $D_c(s)$ and $D_d(s)$ represent the transfer functions for the common and difference mode from sensors to eyes. Clearly, so long as the premotor projection weights are unequal (as occurs in VOR, [7]), then bilateral sensory patterns will drive combined vergence and version responses – both motor strategies could arise from the same control network. In contrast, a pure difference between bilateral premotor signals (PM_R-PM_L) could be used to drive say the head (the support platform), so that only the difference mode would be shared by eyes and head during rotation in the horizontal plane. This is the approach used by our recent model of eye-head coordination [12] which produces eye-head trajectories compatible with behavior during both head-free target pursuit and orienting saccades [6]. In this case a shared premotor circuit can control multiple platforms so long as the imbedded modes are selected by appropriate signs/weights in motor projections.

C Fusing Sensory Modalities

In terms of binocular control in the horizontal plane, all the necessary degrees of freedom (2) are imbedded in the symmetric Equ. 1. The problem then reduces to providing adequate sensory input patterns that will automatically force the required binocular strategy via a relationship like Equ.4. One approach might combine all sensory inputs at the same summing junction in Fig. 3 to create a 'lumped' sensory signal on each side (with different afferent weights). However this would not work in general. Sensors have different processing dynamics and various reflexes have different overall bandwidths. As a result, many models combining say canal and otolith signals rely on separate pre-processing of sensory afferent signals before projecting onto the shared premotor circuit [e.g. 11].

Yet, a shared premotor network need not imply identical sensory-motor dynamics. Sensory projection sites can be selected to produce the desired overall transfer function for each reflex without preprocessing.
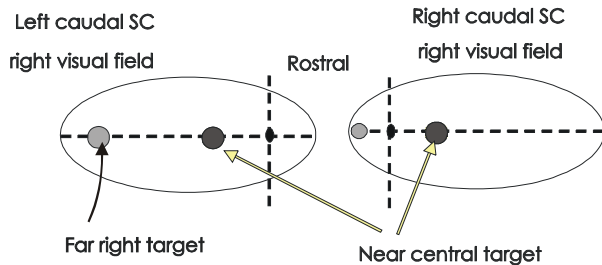

Fig. 4: Bilateral symmetry in visual signals on Superior Colliculi (SC)

In oculomotor control, is well known that different sensory signals project to different points in the premotor circuit: for example, the location of visual targets on the maps of the superior colliculi (SC) are passed via tecto-reticular cells to motor nuclei and the prepositus hypoglossi (PH), signals from the semicircular canals can project directly to the VN (head rotation), but signals from the utricles coding horizontal head acceleration project to different premotor VN cells [see review in [5]).

However it is noteworthy that in all cases, topological symmetry in sensory afferent projections is preserved! Fig. 4 illustrates this for the SC, where the caudal areas respond to targets in the opposite visual field, while the rostral areas contain the foveal zone: there is spatial symmetry along the horizontal meridian coding horizontal eye movements. Thus a far target on the right would appear on the left caudal SC and more weakly on the right rostral SC, while a central near target (while fixating at infinity) would appear on both colliculi at homologous sites. The SC code sensory targets on a neural map, and certainly there are issues of spatial-temporal mapping to motor signals, and the fact that several sensory sources (visual, auditory, somatosensory) are merged there. These are covered elsewhere in this session [1,9], and we focus here on the pattern of sensory projections.
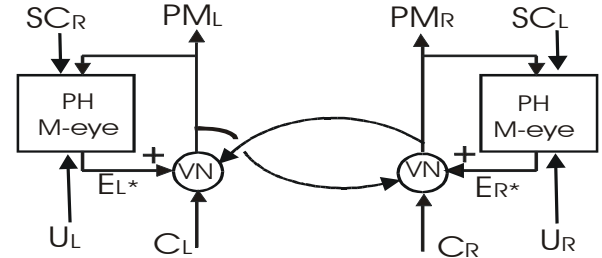

Fig. 5: Selecting appropriate sensory projection sites, while preserving bilateral symmetry.

Fig. 5 is modified from Fig. 2 to include several sensory sources, instead of the generic sensory sources $(S_{R,L})$. The signals from the SC project to PH on the opposite side, a different site from that of canal projections $(C_{R,L})$ to VN. Similarly, the signals from utricles $(U_{R,L})$ enter the symmetric circuit at another site, but symmetrically. Changing sensory projection sites is equivalent to changing the zeroes in Equ. 1.

$$PM_R = \frac{(Ts+1)}{(T_c s+1)} \sum_i \{(S_{Ri}+S_{Li}) G_{ci}(s)\} + \frac{(Ts+1)}{(T_d s+1)} \sum_i \{(S_{Ri}-S_{Li}) G_{di}(s)\} \quad (5)$$

$$PM_L = \frac{(Ts+1)}{(T_c s+1)} \sum_i \{(S_{Ri}+S_{Li}) G_{ci}(s)\} - \frac{(Ts+1)}{(T_d s+1)} \sum_i \{(S_{Ri}-S_{Li}) G_{di}(s)\}$$

This is expressed in Equ. 5, where the subscript 'i' refers to one of the sensory modalities. The circuit always provides dual modes to any sensory input, which will again appear mixed on central activities. This approach has been demonstrated to account for both central and ocular responses during head rotation or translation in the dark, and for responses during mixed vergence-version tasks [2,5]. Note that sensory-specific dynamics can thus be provided for each reflex pair and each mode!

D Mapping Sensory Patterns onto Desired Modes

Though appropriate reflex dynamics can be shaped in a shared premotor circuit, there remains to verify that this circuit will also provide the appropriate motor *strategies* for each sensory case. Here it becomes clear that the pattern of sensory inflow on a shared circuit can suffice to elicit a distinct motor pattern.

Examples can be drawn again from binocular control, assumed driven by a symmetrical circuit as in Fig. 5. During pure head rotation in the dark, or during head translation inter-aurally (side-to-side) while viewing a far target, or while tracking a far target moving horizontally, all the associated sensory signals are reciprocal, increasing on one side and decreasing on the other (zero sum). Thus in Equ. 5, all ocular responses will be forced to follow the difference mode and produce version as required. In contrast, during fore-aft horizontal head translation, the utricular signals on both sides are identical, due to otolith physiology; similarly during pursuit of an approaching central target, activity on both colliculi would be similar. Here the common mode in Equ. 5 survives, and the eyes would perform a pure vergence. Clearly, mixed sensory patterns should produce mixed and appropriate ocular trajectories. The key here is that the geometry of sensory connectivity can take advantage of the topology and modes of the premotor network. Motor strategies represent an unmasking of centrally imbedded modes, by sensory patterns.

III DISCUSSION

An alternative to the classical theories for platform coordination, and the selection of motor strategies has been presented. This was illustrated with a simple bilateral structure imbedding only two modes in a given context. Yet this simple two-mode example can provide multiple motor strategies, based either on hard parameter switching (nystagmus example), or on smooth parametric changes caused by the non-linear behaviour of central cells (saturating non-linearities).

An initial study of the stretch reflex has shown that intersegmental circuits in the spinal cord could also imbed co-contraction and movement signals for a simple joint [8]. In addition, the joint set-point (context) can cause on-line reflex changes, especially if the parametric weights in a topologically symmetric circuit are not themselves identical. Use of asymmetric parameter weights in a symmetric topology can allow cross-talk between modes when desired. As a result it is possible for example to cause mixed vergence/version responses during pure head rotation (differential drive), as required for the ideal VOR while viewing close targets.

IV. CONCLUSION

Studies on the networks for oculomotor control indicate that a single premotor network with a symmetric topology can provide*:*
- One-step sensory fusion and sensorimotor transformations
- Imbedded multiples modes (tasks, or trajectories)
- Selectable modes for platform coordination
- Context-sensitive behaviour caused by set-points in non-linear premotor circuits.

The secret is in the appropriate tuning of network topology, which provides a capacity to imbed *locally* several motor strategies, simply released by the current context and sensory inflow patterns. This is in contrast to the classical approach where desired motor patterns are selected at a cortical/spinal level, selecting from stored alternatives after several computational stages. Instead, circuit topology should be considered a key element in the process of sensorimotor mapping and in the selection or storage of motor strategies.

These results are relevant for spinal motor control of multiple joints. Given the regularity of intersegmental spinal circuits, and their multiple levels of symmetry, one might expect that a large number of complex modes could be imbedded to provide a rich dictionary of limb trajectories [4]. One could imbed as many motor patterns as there are lines of topological symmetry. Now the challenge is to probe the relative contributions provided by central controllers (cognitive), sensory-motor mapping, and peripheral plant dynamics. In biology, the inherent interconnectivity between these processes, and the topological symmetry of many centers, point to fused imbedded solutions in a distributed system. Clearly the network *structure* is part of the solution and must be taken into account.

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